Human observers impact habituated samango monkeys' perceived landscape of fear

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Short title: Observing the landscape of fear

Abstract: Humans and human infrastructure are known to alter the relationship between predators and prey, typically by directly or indirectly shielding one of the species from the other. In addition to these overt changes to animals' behavior, observers may have more subtle impacts on animals' foraging decisions. However, the anthropogenic alteration of risk-taking behavior has rarely been acknowledged or quantified, particularly in behavioral ecological studies reliant on habituated animals. We tested the magnitude of the "human shield effect" experimentally on two groups of samango monkeys, *Cercopithecus mitis erythrarcus*, at a site with high natural predator density and no human hunting pressure. In general, giving up densities (GUDs) – the density of food remaining in a patch when a forager leaves – were greatest at ground level (0.1m) relative to three tree canopy levels (2.5m, 5m and 7.5m), highlighting a strong vertical axis of fear. When human followers were present, however, GUDs were reduced at all four heights; furthermore, for one group, the vertical axis disappeared in the presence of observers. Our results suggest that human observers lower monkeys' perceived risk of terrestrial predators and thereby, affect their foraging decisions at or near ground level. These results have significant implications for future studies of responses to predation risk based on habituation and observational methods.

Lay Summary: Wild animals make trade-offs between food and safety. Using an experimental approach, we show that habituated arboreal monkeys at a predator-rich site feel safer in the presence of human observers. Specifically, they exploit more food at and near ground level, altering their typical anti-predator responses. Research on risk-sensitive behavior thus needs to account for observers' influence on mammals' landscape of fear, and employ indirect and experimental methods in combination with, or instead of direct observations.

INTRODUCTION

Many studies of behavioral ecology rely on the habituation process for the collection of detailed observational data on focal species. After repeated and non-threatening contact with humans, we often assume that animals' behavior becomes relatively independent of our presence (Crofoot et al. 2010). However, human observers are known to influence naturalistic interactions, for example between predators and prey by changing prey animals' behavior including routine anti-predator activities, or by affecting the timing and frequency of predation attempts (Isbell and Young 1993; Stanford 1998; Berger 2007; Meshesha 2013). These effects are a manifestation of predators and prey tending to respond differentially to human activity (Ngoprasert, Lynam, and Gale 2007; Rogala et al. 2011). For example, in Gombe National Park, Tanzania, red colobus monkeys (*Procolobus badius tephrosceles*) fled human observers following habituated chimpanzees (*Pan troglodytes schweinfurthii*), which in turn used this "flushing" of colobus by humans to capture the panicked monkeys (Stanford 1998). Isbell and Young (1993) observed a higher rate of predation on vervet monkeys (*Chlorocebus aethiops*) by leopards (*Panthera pardus*) in Amboseli National Park, Kenya when observers were away from the field site, suggesting that observers shield habituated monkeys from ground predators. The potential impact of "non-invasive" observers on small-scale anti-predator responses of prey animals (such as alarm calling, or abandoning food to seek shelter) is seldom explicitly considered in behavioral ecological research, even though the "human shield effect" (Berger 2007) can bring about broad-scale changes in the distribution and movement patterns of prey and predator species.

Quantitatively assessing subtle changes in animals' behavior due to the presence of human observers can be challenging, particularly in matching conditions with and without

observers present. The amount of food that a forager leaves behind in an experimental food patch, the "giving up density" (GUD), provides one technique for measuring animals' perceived risk without the need for human observers (Brown 1988; Tadesse and Kotler 2012). Animals are predicted to feed more intensively in areas where they feel safe, and relatively lower GUDs indicate preference for a specific area or food patch (Brown 1988; Verdolin 2006). In addition to reflecting trade-offs between resource use and predation risk, GUDs reflect "missed opportunity costs," activities foregone while foraging in a patch (Brown 1988). A forager should cease feeding in a depletable food patch when the value of its harvest rate (*H*) no longer exceeds the sum of its energetic cost of foraging (*C*), predation risk (*P*) and missed opportunity cost (*MOC*): $H = C + P + MOC$ (Brown 1988).

GUDs have been used to measure foraging effort under predation risk in a variety of taxa such as rodents (Brown 1988; Baker and Brown 2010), marsupials (Stokes et al. 2004) and domestic goats (*Capra hircus*) (Shrader et al. 2008). The method has a range of applications, including the assessment of avian microhabitat preferences (Oyugi and Brown 2003), the impact of tourism on Nubian ibex (*Capra nubiana*) (Tadesse and Kotler, 2012), and how arboreal primate species perceive predation risk in both the horizontal and vertical dimensions (Emerson, Brown, and Linden 2011). In samango monkeys (*Cercopithecus mitis erythrarcus*), GUDs decrease with height, highlighting a strong vertical axis of fear in this species (Emerson, Brown, and Linden 2011) as opposed to the horizontal axis (sightlines and vegetation cover) more typical of semi-terrestrial primates such as vervet monkeys (*Chlorocebus aethiops*) (Makin et al. 2012). Importantly, the GUD method allows researchers to quantify prey animals' risk-taking behavior without the need for direct observation.

We used GUDs and vertical arrangements of feeding stations (similar to Emerson, Brown, and Linden 2011) to compare the depletion of artificial foraging patches by two groups of samango monkeys in the presence and absence of human observers. We expected that human observers should modulate monkeys' typical responses to predation risk. The baseline response was assessed in our first prediction: an increase in GUDs at lower and upper stations in response to higher perceived predation risks from terrestrial and aerial predators respectively (Emerson, Brown, and Linden 2011). Anthropogenic changes to this baseline anti-predator response were predicted as follows: monkeys would exhibit lower GUDs on days when observers are present. Since humans are terrestrial, the "shielding" effect would be more pronounced in feeding stations closer to the ground, as reflected in differential changes in GUDs along the vertical axis. Finally, monkeys were expected to improve in patch exploitation over the course of the experiment, with each additional visit day, a reflection of increased experience with the specific experiment (Emerson and Brown 2013).

METHODS

The study species

The samango monkey (*Cercopithecus mitis erythrarcus*) is an arboreal guenon confined to forests in southern Africa, the southernmost range extent of the polytypic *Cercopithecus mitis* (Lawes 1990). Samango monkeys are medium sized monkeys (adult females ~4.4kg, adult males ~7.6kg) that form single-male, multi-female groups), with group sizes ranging from 4-65 (Lawes, Cords, and Lehn 2011). The diet of samango monkeys is primarily frugivorous, but also incorporates leaves, insects, and flowers (Lawes, Henzi, and Perrin 1990; Lawes 1991).

The study area

The study was conducted at the Lajuma Research Centre, in the Soutpansberg Mountains, South Africa (23º02'23''S, 29º26'05''E) (Fig. 1). Local climate is temperate/mesothermal, with cool dry winters from April-September and warm to hot wet summers from October-March (Willems, Barton, and Hill 2009). The study area has natural fragments of tall forest (10-20m height) occurring amongst areas of natural short forest (5-10m height). Confirmed predators of monkeys at this site include leopard (*Panthera pardus*) (Chase Grey, Kent, and Hill 2013), as well as caracal (*Caracal caracal*), crowned eagle (*Stephanoaetus coronatus*), African black eagle (*Aquila verreauxii*) and African rock python (*Python sebae*) (Willems and Hill 2009; Ian Gaigher, pers. comm. 2013; Coleman and Hill 2014). Terrestrial carnivores are ambush hunters, leading to stronger risk responses close to ground level, while aerial predators increase primates' predation risk close to the canopy (Seyfarth, Cheney, and Marler 1980; Emerson et al. 2011). Sympatric diurnal primates are chacma baboon (*Papio ursinus*) and vervet monkey (*Chlorocebus aethiops*). There is no hunting of primates at this site, and since the monkeys forage naturally, without access to crops, there is no human-wildlife conflict or anthropogenic persecution of the monkeys. Leopards face persecution from landowners below the mountains for perceived livestock depredation, and are also subject to legal and illegal hunting in parts of the Soutpansberg (Chase Grey 2011; Chase Grey, Kent, and Hill 2013) such that the leopard population is likely to be wary of humans in this environment.

Field experiments

We studied two habituated samango groups during the winter (dry) season from May to August 2013. "Barn" group (40 individuals) has been regularly followed since September 2009, while "House" group (60 individuals) has been under systematic observation since July 2011. This

115 persistent contact with study groups has resulted in their habituation to people, i.e. a reduction in
116 fear of human observers (Williamson and Feistner, 2011), presumably allowing the study
117 subjects to exhibit their natural behavioral patterns despite the presence of observers. "Follows"
118 were observation sessions in which single observers followed groups from dawn until dusk to
119 conduct standard behavioral data collection independent of our particular experiment. Groups
120 were not followed every day, but an average of 3-4 days per week. We exploited this "natural"
121 variation in observer presence, using follow days as a predictor variable throughout our study.
122 We generated 16 random points (8 per group) within the groups' exclusive winter ranges
123 (outside the groups' range overlap area), mapped using data from the previous year, and selected
124 emergent trees within 20m of those points based on tree characteristics (height 11-12m, with
125 diameter at breast height >25cm) and habitat type (semi-deciduous forest bordering tall
126 evergreen mist-belt forest) (Fig. 1). Group arrays were placed roughly equidistant from a known
127 crowned eagle perch, although the Barn group array was relatively closer to the active crowned
128 eagle nest-site (Fig. 1). Eagle calls were heard almost daily from both groups' ranges. Ground
129 predators (leopard and caracal) were captured on camera traps visiting the covered GUD basins
130 during the night in groups' ranges.
131 We modified methodology from Emerson, Brown, and Linden (2011), who previously
132 validated the GUD protocol for studying samango monkey ecology at our site. We established
133 artificial foraging patches at each tree, consisting of plastic basins covered with a rope mesh to
134 reduce access and so slow foraging rates, suspended at 0.1m, 2.5m, 5.0m, and 7.5m (four basins
135 per tree, one basin at each height). The 0.1m basin level predominantly tested terrestrial
136 predation risk and the 7.5m basin level, just below the canopy, tested risk from eagles. Basins
137 were filled with 4 litres of sawdust, "baited" with 25 shelled peanuts before 07:00, and sieved

after 16:00 on each of 20 experimental days (4 consecutive days per week for 5 weeks). We recorded the number of peanuts left (the GUD) and the amount of sawdust spilled (in litres) from all four basins at each tree (n=64 basins, 32 per group over 20 days), topping off any spilled sawdust so that each basin contained 4L at the start of the next experimental day. We also noted if researchers were following the monkeys that day for observational data collection. On follow days, human observers were present at or in the vicinity of the feeding stations, but did not actively interfere with monkeys' foraging behavior. Barn group visited GUD stations on 20/20 days, of which 8 were follow days, and House group visited trees on 17/20 days, of which 11 were follow days. On non-follow days and in the absence of observers in the GUD areas, camera trap data confirmed that no other animals visited GUD stations, as was found in Emerson and Brown's study at this same site (2013).

Data analysis

Examination of the numbers of peanuts remaining in basins revealed significant variation throughout the study period (Fig. S1). This created a statistical analysis challenge, as the experimental design created three scales at which random processes were likely to influence GUD variation. Firstly, the trees onto which we placed our basins may have varied in their perceived risk due to subtle differences in, for example, canopy cover and understory foliage density (Emerson and Brown 2013). Secondly, basin utilization may have varied between days due to variation in environmental factors that influence risk (e.g. cloud cover), which could affect all monkeys equally on a given day. Thirdly, the utilisation of basins on a tree on a given day may have varied stochastically due to local chance events that may impact individual monkeys differentially (e.g. a monkey becoming startled). It is important that these biologically

relevant sources of stochastic variation are accounted for in the statistical analysis because ignoring them could lead to inflated type I errors (Richards 2008). As we could not find a statistical package capable of explicitly describing the above-mentioned correlated variance structure (including GLMMs), we instead developed a likelihood function linking the experimental design with our hypotheses on the effect of environmental factors and observation on risk-taking behavior (see equation 2). Specifically, we developed a model that allowed us to look for evidence that GUDs were influenced by basin height (Z), the presence of human followers that day (F), and the number of days the tree had been previously visited during the study (V). For a basin placed at height z_k on tree i, the logit-transformed probability that each peanut remained in the basin on sampling day j was described by:

$$\text{logit}\ \bar{p}_{ijk} = (\beta_0 + \beta_{\text{F}} x_{ij}) + (\beta_{\text{Z}} + \beta_{\text{ZF}} x_{ij}) z_k + (\beta_{\text{V}} + \beta_{\text{VF}} x_{ij}) v_{ij}, \quad (1)$$

where v_{ij} is the number of days the tree had previously been visited, x_{ij} indicates if the group was followed that day (0 = no, 1 = yes), and the β are model parameters describing effect sizes. The three above-mentioned sources of variation were included by considering the following likelihood function:

$$L(\boldsymbol{\theta}|\text{data}) = \prod_{j=1}^{20} \int_{u=-\infty}^{\infty} f_{\text{n}}(u|0,1) \prod_{i=1}^{8} \prod_{k=1}^{4} f_{\text{bb}}\left(y_{ijk}|25, T[\bar{p}_{ijk}, u\sigma + w_i], \phi\right) du, \quad (2)$$

where $\boldsymbol{\theta}$ is the set of parameters that define the statistical model, $f_{\text{n}}(u|0,1)$ is the density function for the standard normal, $f_{\text{bb}}(y|N,p,\phi)$ is the beta-binomial distribution with variance parameter ϕ (Richards 2008), and $T[\bar{p},\tau] = e^{\lambda}/(1+e^{\lambda})$ where $\lambda = \ln\left(\bar{p}/(1-\bar{p})\right) + \tau$. Potential

differences in tree affinities (i.e. the first source of stochastic variation) were included by associating each tree *i* with a parameter w_i (a positive value indicates that, on average, more peanuts were left in the tree's basins throughout the study). The transformation *T* ensures that the probability a peanut remains in a basin when placed in a specific tree on any day is bounded by (0, 1). The standard normal distribution accounts for the second source of variation (a positive *u* indicates that GUDs were higher than average on that day), with the degree of daily variation quantified by □. The third source of GUD variation mentioned is accounted for by incorporating the beta-binomial distribution. We found that the likelihood function described by equation (2) was able to describe the structured variation in peanut numbers observed (Fig. S1).

Data were effectively excluded for non-visit days by setting f_{bb} to 1, i.e., on days when a tree was not visited, as these conditions provide no information on GUDs. Further, we also set f_{bb} to 1 when more than 1L of sawdust was spilled from a basin (2.9% of basins). These non-visits and excessive spillage occurred at a very low rate, and preliminary analyses indicated that these events were random and thus unlikely to cause significant parameter bias. The Barn and House groups' feeding behavior was inferred using GUDs from 590 and 463 basin samples, respectively (32 basins x 20 experimental days yielded 640 maximum possible samples). Models describing patterns of foraging by the Barn and House groups were coded according to equations (1) and (2) and fit using maximum likelihood. For both groups, we used likelihood ratio tests (LRTs) to look for statistical evidence that the parameters describing the effects of factors: F, Z and V, differed from zero. Specifically, the importance of each of these three factors was evaluated by comparing the full model with the model that removed the factor of interest. A human shield effect is inferred if factor F is deemed statistically significant and GUDs are reduced in the presence of a follower. In this case, the statistical significance of factors Z and V

reveals how followers modulate the monkeys' vertical axis of fear and their propensity to change their level of fear over time.

RESULTS

Both groups of samango monkeys responded in the predicted way to terrestrial, but not aerial, predation risk. The presence of followers modulated one group's baseline responses to potential risk from ground predators. The likelihood ratio tests, when applied to the Barn group data, indicated that GUDs varied with height and the presence of a follower but not with the number of days that the tree had been visited by the group during the study (Table I). GUDs were reduced with increasing height on days when the group was not followed, but GUDs remained low at all heights when the group was followed (Fig. 2A,C). Like Barn group, GUDs of House group were also influenced by basin height and observer follows; however, GUDs were also influenced by tree experience (Table I). For House group, GUDs tended to decrease with height, were lower when the group was followed, and became lower the more the tree was visited (Fig. 2B, D). Importantly, the height effect on GUDs would not have been detected for Barn group if the analysis only included data taken from days the group were followed (Table I; Fig. 2A). In other words, while in the House group the effect of basin height on GUDs remained detectable in the presence of observers, in the Barn group the height effect disappeared when observers were present suggesting that a vertical axis of fear would not have been detected if the group was always followed. In general, Barn group had lower GUDs than House group (Fig. 2). Table S1 provides the maximum likelihood parameter estimates for each of the models presented in Table I.

DISCUSSION

Our results suggest that human observers can alter the vertical axis of fear in habituated, arboreal monkeys. As predicted, we found a strong vertical axis of fear, consistent with Emerson, Brown, and Linden (2011), with monkeys depleting the least food at patches near ground level. More significantly, however, monkeys' variation in perceived risk along this vertical gradient was affected by the presence of human observers (Fig. 1). This effect was most apparent at lower levels in the tree, suggesting that behavioral researchers were perceived as shields against terrestrial predators in particular. We speculate that this observed pattern may be due to humans passively deterring predators from the immediate area, rather than playing the role of active sentinels. This is consistent with findings from ungulates, where mountain nyala (*Tragelaphus buxtoni*) avoid hyenas (*Crocuta crocuta*) by over-nighting next to human settlements (Meshesha 2013), and moose (*Alces alces*) avoiding calf depredation by brown bears (*Ursus arctos*) by birthing near to human infrastructure (Berger 2007). In our case, monkeys did not actively seek out humans to avoid predators, although monkeys' tolerance of human followers could in part be due to anti-predator and other perceived benefits (e.g. displacement of other groups not habituated to humans).

Contrary to predictions from the "Group Size Effect", which posits that larger groups perceive themselves as less vulnerable to ground predators and are expected to deplete more food in risky areas (Quenette 1990; Miller 2002; Makin et al. 2012), overall GUDs were lower (more food was depleted) by the smaller Barn group. This discrepancy may be explained by this group's greater prior experience with both observers and GUD experiments (Emerson, Brown, and Linden 2011; Emerson and Brown 2013). In contrast, the less experienced House group showed an expected response to increasing experience with GUDs reducing with repeat visits, although GUDs decreased more rapidly in the presence of observers. These results suggest that

246 even a slight difference in experience with human observers can affect subjects' behavior and
247 that GUD experiments themselves – and animals' learning of foraging tasks – may influence
248 future experiments (Dukas 2008). Even though future experiments may yield lower GUDs due to
249 past experience, it seems that GUDs, nonetheless, are able to measure differences between
250 treatments, such as height.

251 Our results add to the growing literature suggesting that observer presence never becomes
252 truly "neutral" to study animals (Jack et al. 2008; Crofoot et al. 2010; McDougall 2012) and
253 highlight the importance of considering the effects that habituation has on animal behavior,
254 particularly where study populations may be at risk from other human activities, for example
255 poaching, poisoning or conflict with agriculturalists (Williamson and Feistner 2011).
256 Importantly, we would not have detected a vertical axis of fear for Barn group if they were
257 always followed (Fig. 2A). If observer presence can significantly alter GUDs in study animals
258 (Fig. 2), and modify the effects of learning/experience, this clearly has important implications for
259 studies of vigilance and predator-prey interactions. Researchers thus need to be cautious in
260 interpreting the effect sizes of predation parameters where the extent of human presence may
261 vary (e.g. Isbell and Young 1993), and use indirect and experimental methods in combination
262 with or instead of direct observation. For example, while behavioral research on the same
263 population of samango monkeys found the landscape of fear from eagles to be the most
264 significant determinant of range use (Coleman and Hill 2014), the study reported no response to
265 the threat of predation from leopards. Further work would be required to determine whether this
266 represents a true reflection of the landscape of fear from terrestrial predators or whether human
267 shield effects influence ranging patterns in the presence of observers. Similarly, habituation has
268 been shown to interact with the effects of risk allocation in blackbirds (*Turdus* merula) in

269 determining flight initiation distances in the face of 'usual' and 'novel' predators (Rodriguez-
270 Prieto et al. 2009). Nevertheless, these insights about fear, behavior and predator-prey
271 relationships can assist conservation managers in understanding how anthropogenic effects
272 influence species distribution, habitat selection and risk-sensitive behavior (Berger 2007).

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Fig. 1 Study area showing locations of 16 experimental trees. Minimum convex polygons represent winter ranges of two samango monkey study groups based on 773 waypoints for Barn group and 695 waypoints for House group from the previous winter. The vegetation map is based on unpublished data. The active crowned eagle nest and common perch site are shown.

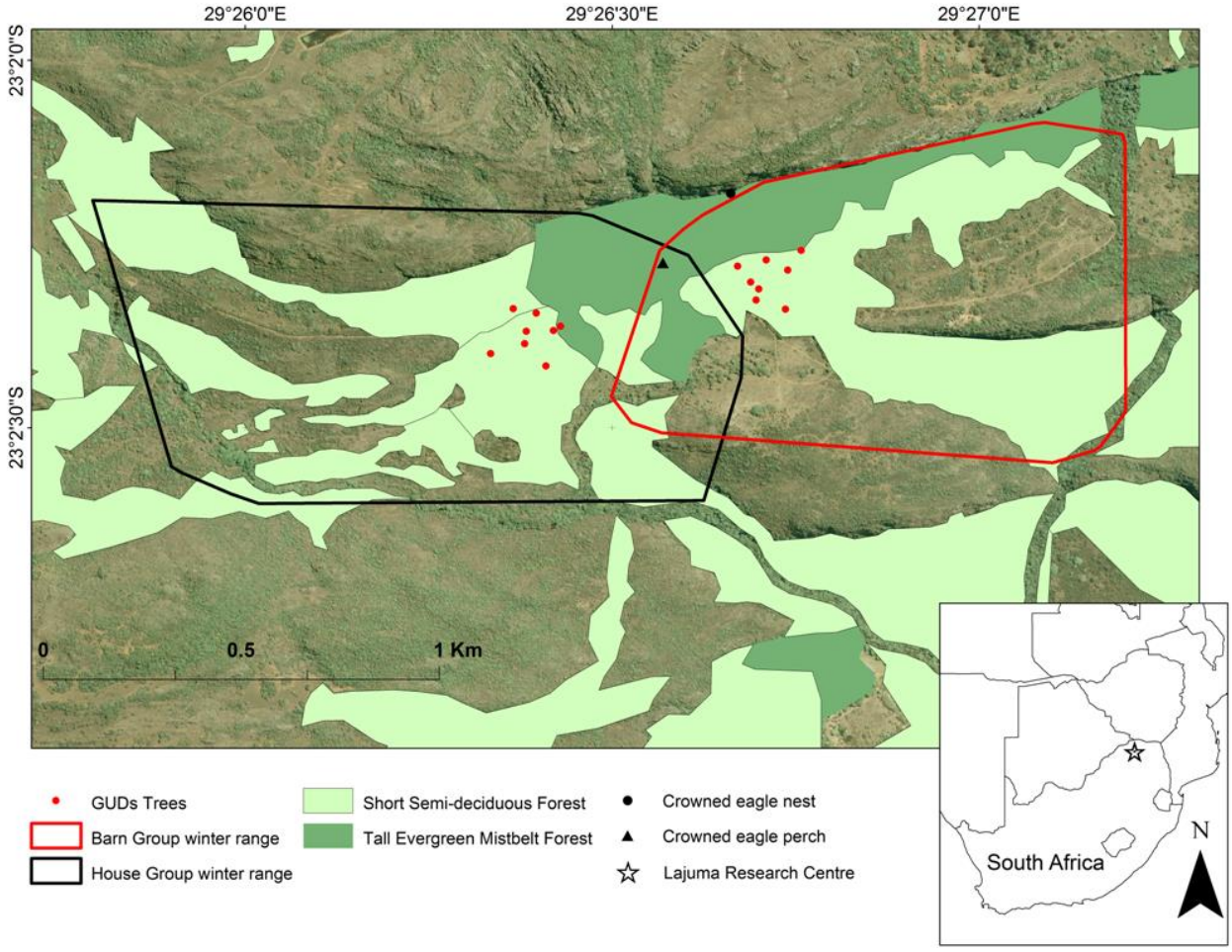


Fig. 2 Observed GUDs for both groups split according to whether or not data were collected on days when the group was followed or not. Panels A and B show basin height effects. Panels C and D show how GUDs change with tree experience for the lowest basins that were hung at a height of 0.1m. Error bars depict 95% confidence intervals, assuming data are drawn from a beta-binomial distribution, and were calculated using the profile likelihood approach.

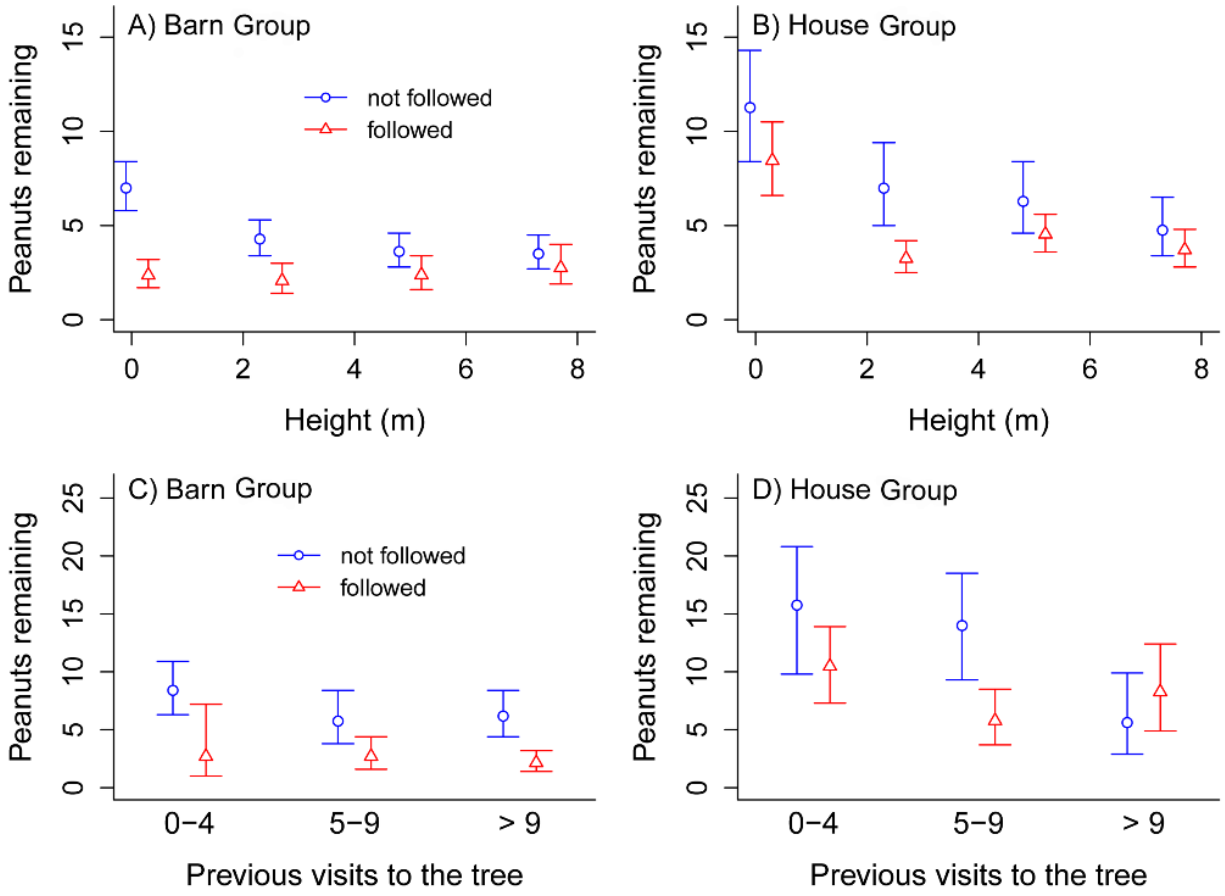


Table I: Summary of the likelihood ratio tests (LRTs) used to look for evidence that GUDs were affected by the presence of a follower (F), the height of the food basin (Z), and the number of days the group had previously visited the experimental tree (V). Results are presented for both groups. The first set of tests considers all data (i.e. days followed and not followed), whereas the second set only examines data collected on days when a group was followed. Factor removed indicates which factor the LRT is testing for statistical significance.

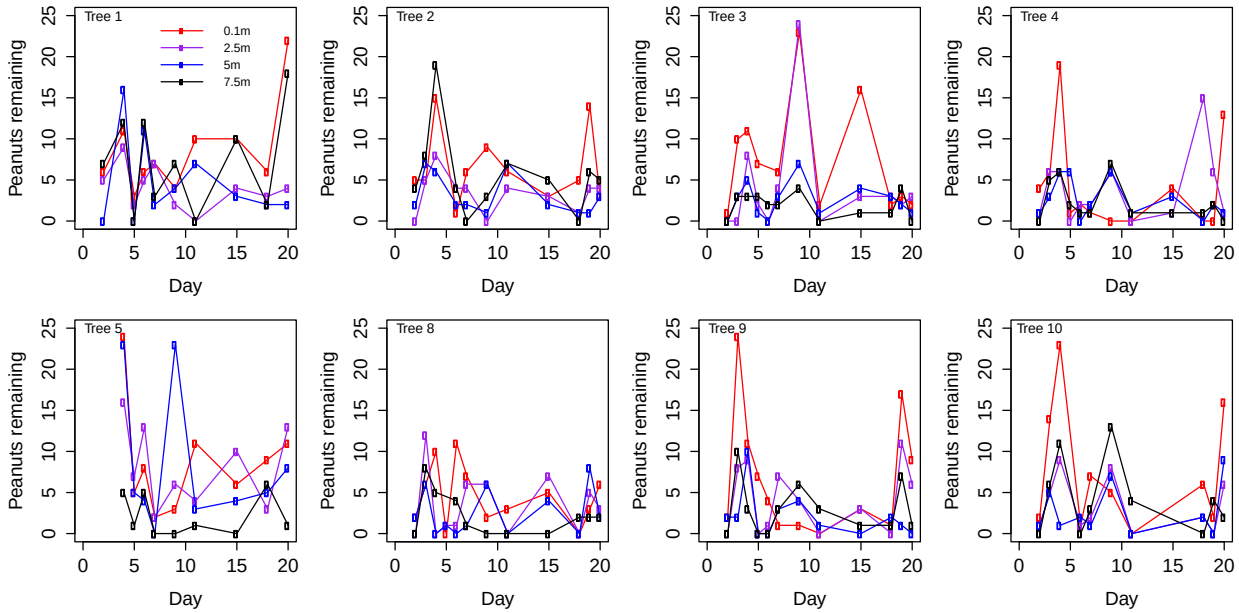
Models compared	**Factor removed**	***G***	**df**	***P*-value**
Barn Group				
Consider days when the group was followed and days when it was not followed				
M(F+Z+V), M(Z+V)	F	14.86	3	0.002
M(F+Z+V), M(F+V)	Z	29.01	2	< 0.001
M(F+Z+V), M(F+Z)	V	0.04	2	0.980
Only consider days when the group was followed				
M(Z+V), M(V)	Z	0.12	1	0.733
M(Z+V), M(Z)	V	0.07	1	0.796
House Group				
Consider days when the group was followed and days when it was not followed				
M(F+Z+V), M(Z+V)	F	10.94	3	0.012
M(F+Z+V), M(F+V)	Z	18.25	2	< 0.001
M(F+Z+V), M(F+Z)	V	9.19	2	0.010
Only consider days when the group was followed				
M(Z+V), M(V)	Z	8.49	1	0.004
M(Z+V), M(Z)	V	0.77	1	0.380

Supplementary Material

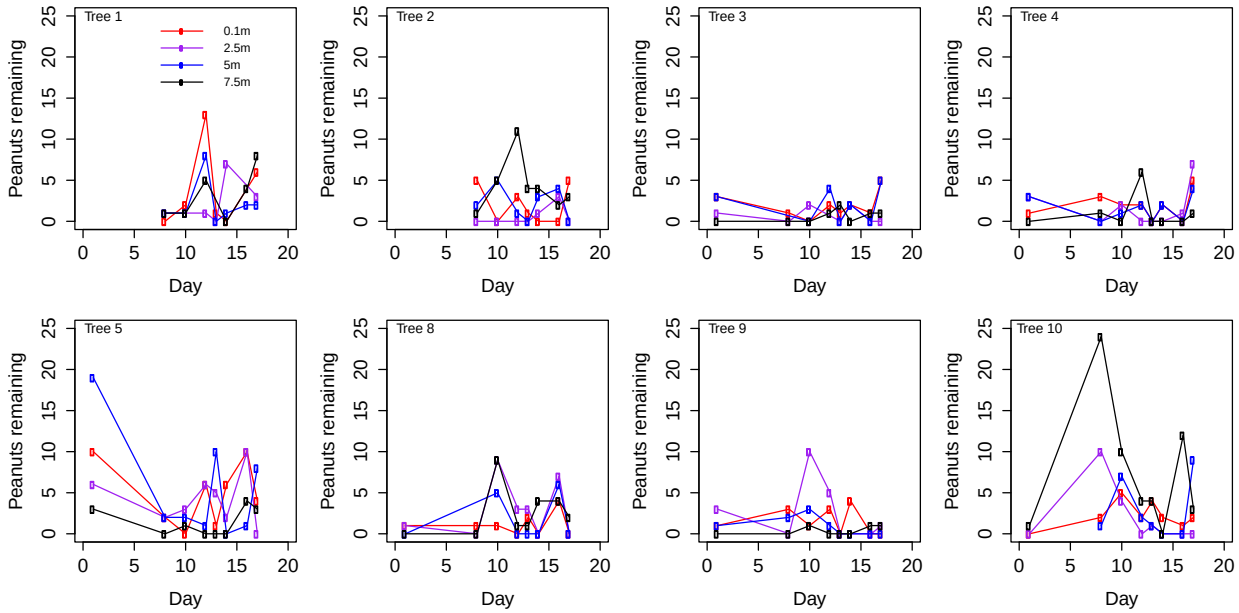
Table S1: Maximum likelihood parameter estimates for models fit to both sets of group data and used for the likelihood ratio tests. Model descriptions that include a Z, F, or V, indicate that GUD is affected by basin height, whether the group is followed that day, and the number of times the tree had been previously visited, respectively. K is the number of model parameters estimated and LL_{max} is the maximum log-likelihood. The seven independent model parameters that describe variation among trees, w_1-w_7, are not presented here. Note that $w_8 = -\sum_{i=1}^{7} w_i$. Fits are presented for both groups. The first set of parameter estimates are for all the data (i.e. days followed and not followed), whereas the second set only examines data collected on days when a group was followed.

	Maximum-likelihood model parameter estimates									
Model	β_0	β_F	β_Z	β_{ZF}	β_V	β_{VF}	ϕ	σ	K	LL_{max}
Barn Group										
Consider days when the group was followed and days when it was not followed										
M(Z+V)	-1.483	0	-0.079	0	-0.011	0	0.160	0.583	12	-1352.1
M(F+V)	-1.519	-0.720	0	0	-0.007	0.004	0.171	0.455	13	-1359.2
M(F+Z)	-1.185	-1.058	-0.110	0.094	0	0	0.156	0.473	13	-1344.7
M(F+Z+V)	-1.163	-1.021	-0.112	0.096	-0.001	0.000	0.157	0.473	15	-1344.7
Only consider days when the group was followed										
M(V)	-2.235	NA	0	NA	-0.007	NA	0.151	0.203	11	-481.0
M(Z)	-2.261	NA	-0.010	NA	0	NA	0.150	0.208	11	-481.0
M(Z+V)	-2.210	NA	-0.010	NA	-0.005	NA	0.151	0.203	12	-480.9
House Group										
Consider days when the group was followed and days when it was not followed										
M(Z+V)	-0.002	0	-0.103	0	-0.098	0	0.371	0.496	12	-1253.0
M(F+V)	-0.002	-1.169	0	0	-0.108	0.087	0.401	0.297	13	-1256.9
M(F+Z)	-0.387	-0.654	-0.120	0.044	0	0	0.371	0.447	13	-1252.1
M(F+Z+V)	-0.002	-0.852	-0.097	0.017	-0.083	0.058	0.372	0.330	15	-1247.5
Only consider days when the group was followed										
M(V)	-1.224	NA	0	NA	-0.016	NA	0.384	0.065	11	-822.5
M(Z)	-1.055	NA	-0.076	NA	0	NA	0.366	0.079	11	-818.6
M(Z+V)	-0.953	NA	-0.075	NA	-0.016	NA	0.365	0.070	12	-818.2

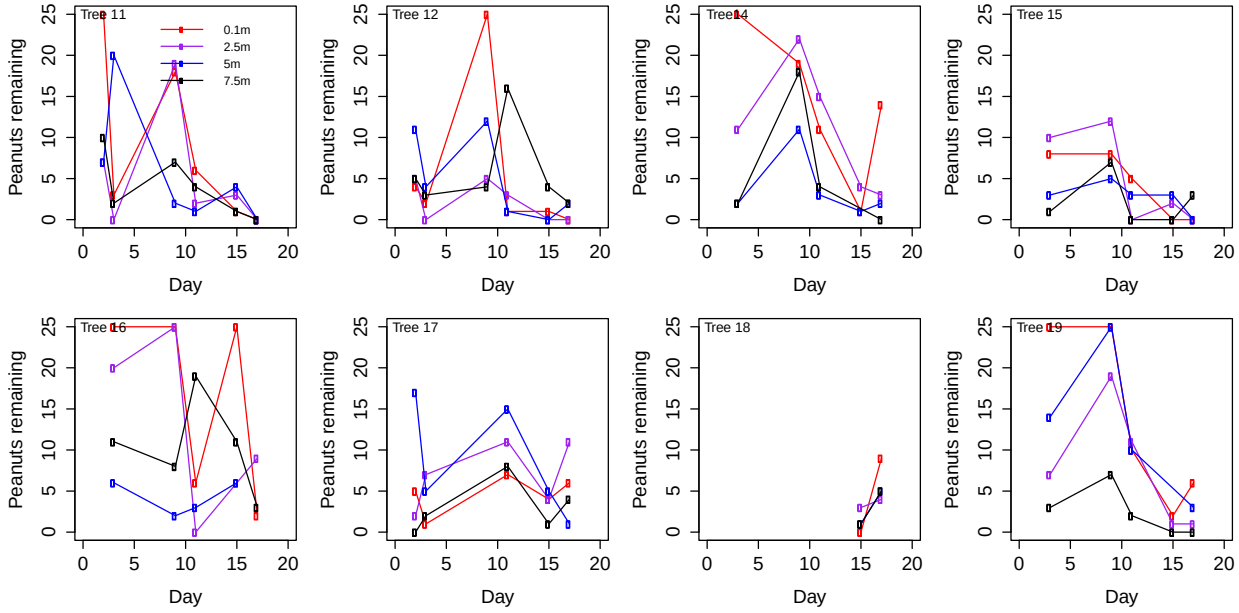
(A) Barn group when not followed



(B) Barn group when followed



(C) House group when not followed



(D) House group when followed

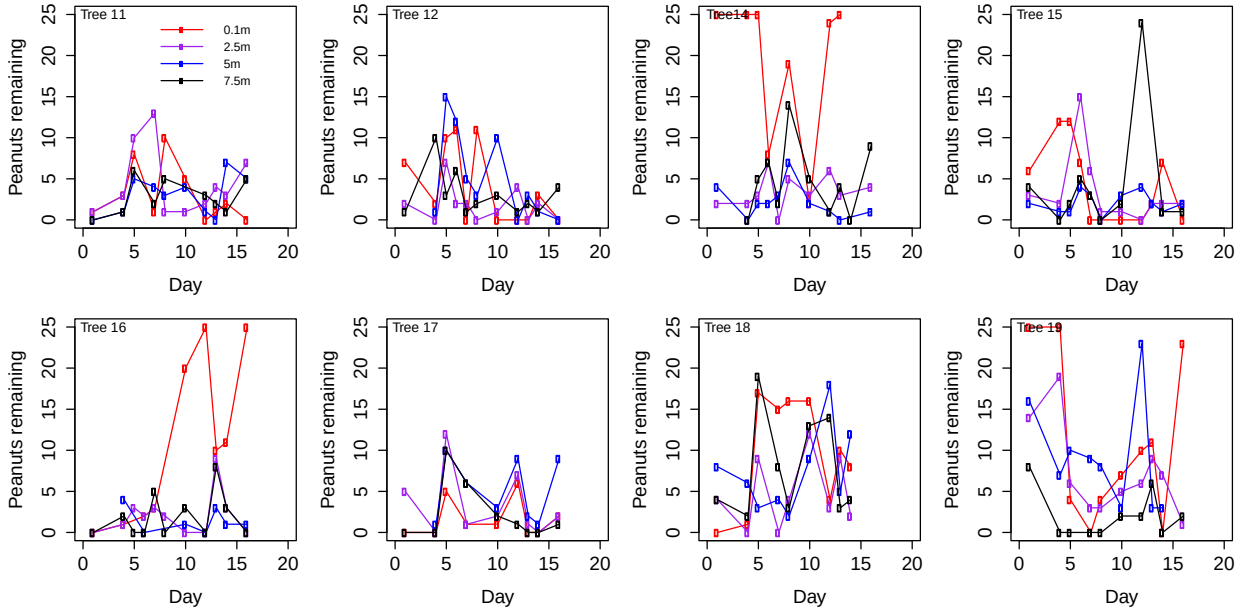


Figure S1: Peanuts remaining in basins for two groups of samango monkeys across 20 sampling days. Note that sampling days span a 5-week period. Data are segregated according to whether or not the group was followed on the sampling day. Each panel depicts peanuts remaining at a specific tree for four basin heights. These data show very high variation in peanut numbers across sampling days and even among basins on a given day, supporting our assumption that the data are beta-binomial distributed. The data also suggest some degree of between-tree variation, which supports our model incorporating tree as a random factor.